

Cryptomya californica (Conrad, 1837): Observations on Its Habitat, Behavior, Anatomy, and Physiology

by

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Abstract. Descriptions and photographs of the estuarine habitat, external and internal structures, and gut contents of the lamellibranch clam *Cryptomya californica* (Myoida: Myidae) are presented. Also included are behavioral observations, and experimental information on the digestive tract and its associated bacteria.

INTRODUCTION

During my studies on spirochete bacteria of the genus *Cristispira* (LAWRY, 1981; LAWRY *et al.*, 1981), which are isolated most frequently from the crystalline styles of various pelecypods and gastropods, few literature references were found to my favorite source of spirochetes, the marine clam *Cryptomya californica* (Conrad, 1837). However, the importance of this small, burrowing lamellibranch in estuarine ecosystems must be considerable, as it is a predominant animal in vast areas of mudflats along the Pacific coast of America from Alaska to Peru (BROWN *et al.*, 1977; HERTLEIN & GRANT, 1972; KEEN, 1971; PETERSON, 1984; WEST *et al.*, 1976; WICKSTEN, 1978).

The majority of information available on *Cryptomya californica* comes from a limited portion of its range (*e.g.*, the central coast of California), and is contained in three articles (MACGINITIE, 1934, 1935; YONGE, 1951). These papers discuss the clam's Monterey Bay habitats, its shell morphology, anatomy, and particle filtering behavior, and its unusual utilization of the tunnels of other burrowing organisms. Curiously, almost nothing has been published concerning the habitats of *C. californica* throughout the rest of its range, its ecological niche, burrowing behavior, digestive physiology, or reproduction.

In this paper, I compare Oregon estuarine habitats of *Cryptomya californica* with those previously described in California. The clam's burrowing behavior is discussed, and pre-existing anatomical data are reviewed, photographically documented, and embellished with new observations about the digestive tract, wandering amebocytes, and gametes. The nature of the clam's food and its processing by the digestive system are investigated. Special problems related to digestion are addressed, such as the function of the crystalline style, how this organ is affected

by tidal rhythms, whether it contains digestive enzymes, and, if so, whether they are of clam or bacterial origin. Also discussed are other possible roles played by the clam's gut-associated bacteria.

MATERIALS AND METHODS

Cryptomya californica was collected from sandy mudflats of Yaquina Bay and Coos Bay, Oregon. Photographic records were made of the habitat, substrate, arrangement of clams around the tunnels of the ghost shrimp *Callinassa californiensis* (Dana, 1854) (see MACGINITIE, 1934), and the burrowing behavior of the clam. In order to determine the nature of the diet, intestinal contents and fecal pellets were obtained from freshly collected clams.

To microscopically observe the internal anatomy of *Cryptomya californica*, de-shelled, whole clams were fixed and dehydrated using a freeze substitution technique. They were then embedded in paraffin and cut into 7- μ m thick sections. These were stained with Harris' hematoxylin and eosin (H and E), and observed and photographed using a Zeiss Universal microscope equipped with a Nikon AFM automatic exposure meter and a 35 mm camera. Brightfield optics were used to make photomicrographs of the digestive organs. Phase contrast was used to demonstrate the presence of *Cristispira* within sections of the crystalline style. Intestinal contents were photographed *in situ* using Nomarski optics.

A clam submerged in seawater was vivisected and photographed through a Nikon SMZ-10 zoom-lens dissecting microscope in order to observe the digestive organs and the direction and periodicity of crystalline style rotation, which could be seen through the nearly transparent wall of the style sac.

To observe the structure of the crystalline style (NELSON, 1918; YONGE, 1932), styles were extracted by making a small incision into the stomach and forcing the style through the opening by exerting light pressure onto the side of the visceral mass. Each style was placed in a drop of seawater, and phase contrast and Nomarski optics were used respectively to photograph amebocytes on the outer surface of the style (MATHERS, 1972; YONGE, 1926) and *Cristispira* within the matrix. Sperm and eggs were collected during vivisections and photographed in seawater using Nomarski optics.

To determine whether populations of spirochetes in *Cryptomya californica* are self-perpetuating, or whether they dwindle after the clams are removed from their natural habitat, the following test was performed. Changes in populations of *Cristispira* within the styles of clams held in aquaria for several weeks were monitored by periodically dissolving a known number of styles in an isotonic saline solution (LAWRY *et al.*, 1981), measuring the total volume, and counting all the spirochetes in 5- μ l portions, using darkfield microscopy. The average number of bacteria per style was then calculated.

To gain further clues as to the roles of the crystalline style in digestion, the possible presence of amylase, a starch-hydrolyzing enzyme common in molluscan styles, was investigated (IORDACHESCU & DUMITRU, 1978; MATHERS, 1973). Styles were analyzed for amylase activity by placing extracted styles, sterilized and washed with toluene, on 0.5% starch/marine nutrient agar culture medium (6 g Sigma no. S-2630 soluble starch, 66 g Difco 2216 marine nutrient agar, 1200 ml distilled water, autoclaved at 121°C for 15 min) for 24 h at 20°C. Hydrolysis of the starch in the medium was checked for by color-developing the plates with Gram's iodine.

To investigate whether gut-associated bacilli can produce amylase, possibly contributing to that stored in the crystalline style, the following experiment was performed. Colonies of Gram-negative, motile bacilli were isolated from the surfaces of extracted, unsterilized styles streaked on to the above-described medium. Their ability to hydrolyze starch was determined by subculturing the bacteria to the same medium, incubating for 24 h at 20°C, and color-developing the plates with Gram's iodine.

The following observations were made to determine whether the style is always present, or whether its presence is affected by fluctuations in tides or food supplies, as in some other intertidal mollusks (LANGTON, 1977; MATHERS, 1974). The presence of styles in freshly collected clams during low tides was noted. Clams removed from seawater for 24 h at 10°C were checked for the presence of styles. *Cryptomya californica* maintained (with food) in aerated seawater (27 to 30‰ salinity, 8°C) for extended periods of time were examined for styles. The effects of 6 weeks of starvation on style production were studied.

To observe the initial distribution of ingested particulate matter within the digestive organs, carmine dye particles (Allied Chemical Corp., National Aniline Div., Biological

Stains Dept., cat. no. 475) were fed to clams. Other clams were given the flagellated unicellular green alga *Dunaliella salina*. The clams were dissected after 1 h, and the digestive organs examined for the location of the ingested carmine particles or algae.

RESULTS

Habitat

Cryptomya californica was easily found in sandy lower estuarine mudflats of Yaquina Bay and Coos Bay, Oregon, during tides lower than +0.3 m (Figure 1a). Individuals were especially prevalent in areas inhabited by the ghost shrimp *Callinassa californiensis* (Figures 1b, c). The clams were usually embedded in the walls of the tunnels of the shrimp (Figure 1d), with only their short siphons protruding into the tunnels. This was sometimes difficult to observe, as the tunnels tended to collapse during excavation. Some specimens, however, were interred with no obvious connection to a tunnel. Often hundreds of clams were found in a square meter of substrate.

Burrowing Behavior

Clams placed on their side on submerged sand began to burrow after a few minutes, if left undisturbed. Burrowing takes place as follows. First, the siphons and large, ciliated foot emerge (Figure 2a). The extended foot can assume shapes ranging from knife-shaped to spade-shaped (Figure 3a), and muscular contractions, along with ciliary action on the outer surface, enable the foot to dig rapidly into the sand. The foot digs directly down into the sand, and when it is firmly anchored, the animal pulls itself off its side onto the anteroventral portion of the shell (Figure 2b). As the foot continues to dig, the entire animal periodically rocks in a dorsoventral plane, and with each rocking cycle the animal works itself deeper into the substrate (Figure 2c). After about 5 min the entire clam, except for the siphons, is completely buried (Figure 2d). Eventually the organism burrows deeper into the sand. How far or fast the clam can dig through the substrate, or how long it can survive without reaching an adequate tunnel was not determined in this study.

Anatomy

Shell morphology: The yellow-white, oblong shells are fragile and small. Although specimens of *Cryptomya californica* greater than 30 mm in length have been reported, the majority of shells collected in this research were less than 20 mm long. The shells gape at the posterior end, and the right valve is slightly fuller than the left. Delicate concentric growth lines are present. A brown periostracum extends beyond the growing shell margin and protects the mantle when it protrudes. The prominent chondrophore (Figure 3b) protruding from the hinge of the left valve is held by an internal resilium in the right valve (ABBOTT,

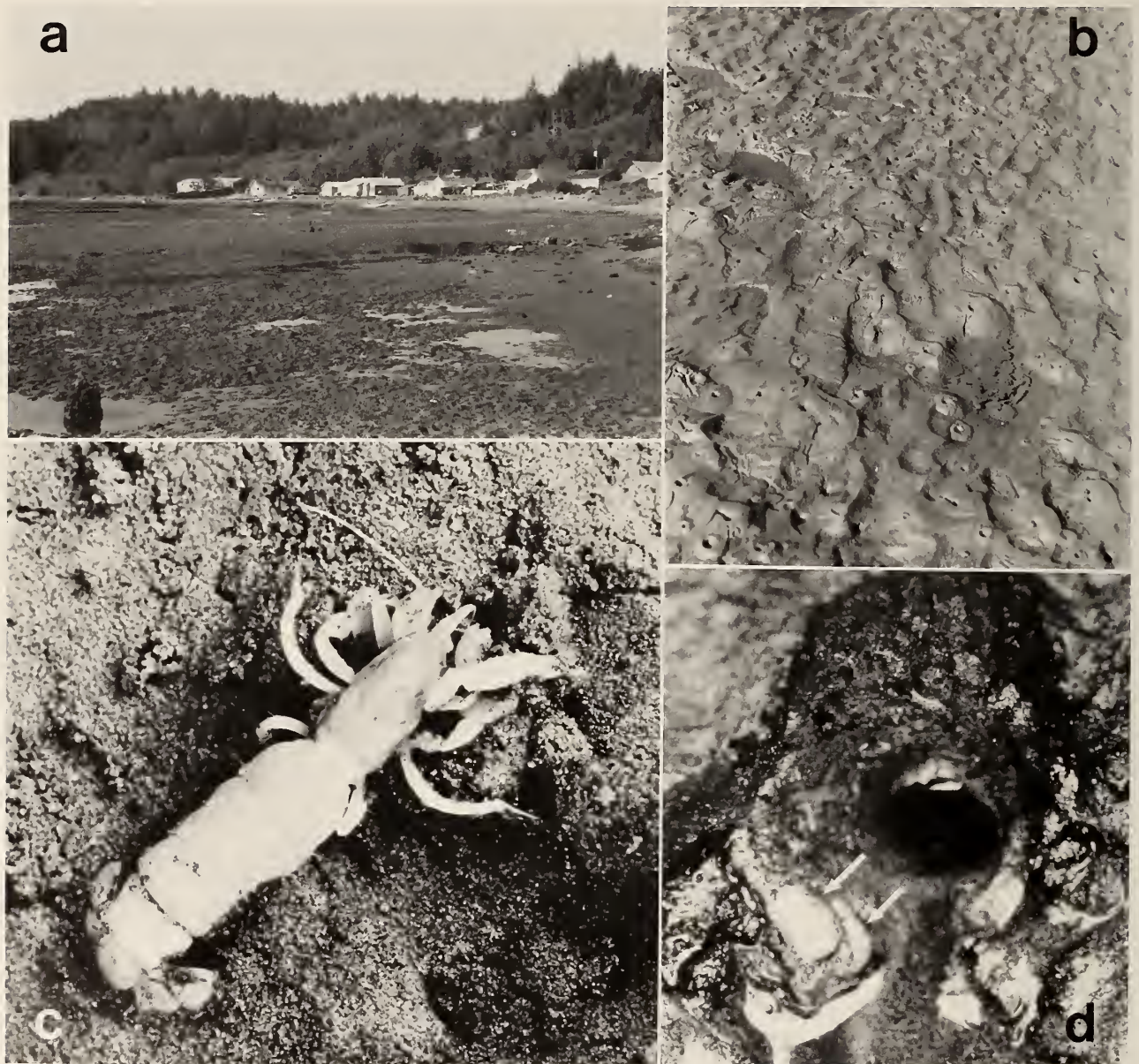


Figure 1

The habitat of *Cryptomya californica*. a. A typical sandy estuarine mudflat, representative of the normal habitat of *C. californica*. Coos Bay, Oregon. b. The usual appearance of the sandy substrate in which lives *Cryptomya californica*, often in proximity to the tunnels of *Callianassa californiensis*. As seen from a height of 1.5 m. c. *Callianassa californiensis* (female, 9 cm in length) burrowing into the sand. d. An excavation of a *Callianassa* burrow showing two *Cryptomya californica* (arrows) with their short siphons oriented toward the tunnel. Found down to depths of 50 cm beneath the surface of the sand, *Cryptomya californica* is usually 1 to 2 cm in length.

1974; HADERLIE & ABBOTT, 1980; QUAYLE, 1973; RUDY & RUDY, 1983).

Siphons: The siphons, as described by YONGE (1951), are extremely short (less than 1 mm in length). A membrane controls the opening of the excurrent siphon, and a row

of tentacles protects the entrance of the incurrent siphon. Both siphons are surrounded by an outer ring of tentacles.

Gills and palps: The relatively large gills (two demi-branches on either side of the body) are covered with cilia, which rapidly pump water through the mantle cavity. The



Figure 2

The burrowing behavior of *Cryptomya californica*. a. A submerged *C. californica* lying on its right side, siphons and foot extended. The foot begins to penetrate the sand. b. When the foot is anchored, the clam rights itself. c. The clam rocks in a dorsoventral plane, and works itself into the substrate. In the gaping posterior portion of the shell are the excurrent siphon (membrane closed) and the incurrent siphon, with its surrounding tentacles. Both are encircled by an outer ring of tentacles. d. After about 5 min the clam is completely buried except for the siphons. The scale in all four photographs is the same. Bar = 1 cm.

cilia also filter food particles from the water and concentrate them into streams of mucus, which are carried to the mouth. Unusable particulate matter is sorted out by the labial palps and condensed into pseudofeces, which are transported by cilia posteriorly along the ventral portion of the mantle, and periodically expelled through the incurrent siphon (YONGE, 1951).

Stomach and intestine: The esophagus and stomach are surrounded by a large mass of digestive diverticula. The intestine emerges from the right side of the stomach, and I found its lumen to be connected for a short distance with the lumen of the style sac. The intestine then winds ventrally toward the posterior portion of the foot, where it

loops dorsally to pass through the heart. The rectum runs dorsally of the posterior adductor muscle, leading to the anus just inside the excurrent siphon (YONGE, 1951).

Crystalline Style

A large style sac extends ventrally from the stomach (Figures 3c, d). The style sac is nearly transparent and has a seamlike structure, comprised of the major and minor typhlosoles, along the length of the right side. I discovered the ventral end of the style sac to be open to the body cavity. Therefore, the organ is actually a tube rather than a sac. The entire inner surface of the sac is lined with cilia, which cause the crystalline style to rotate and to press its

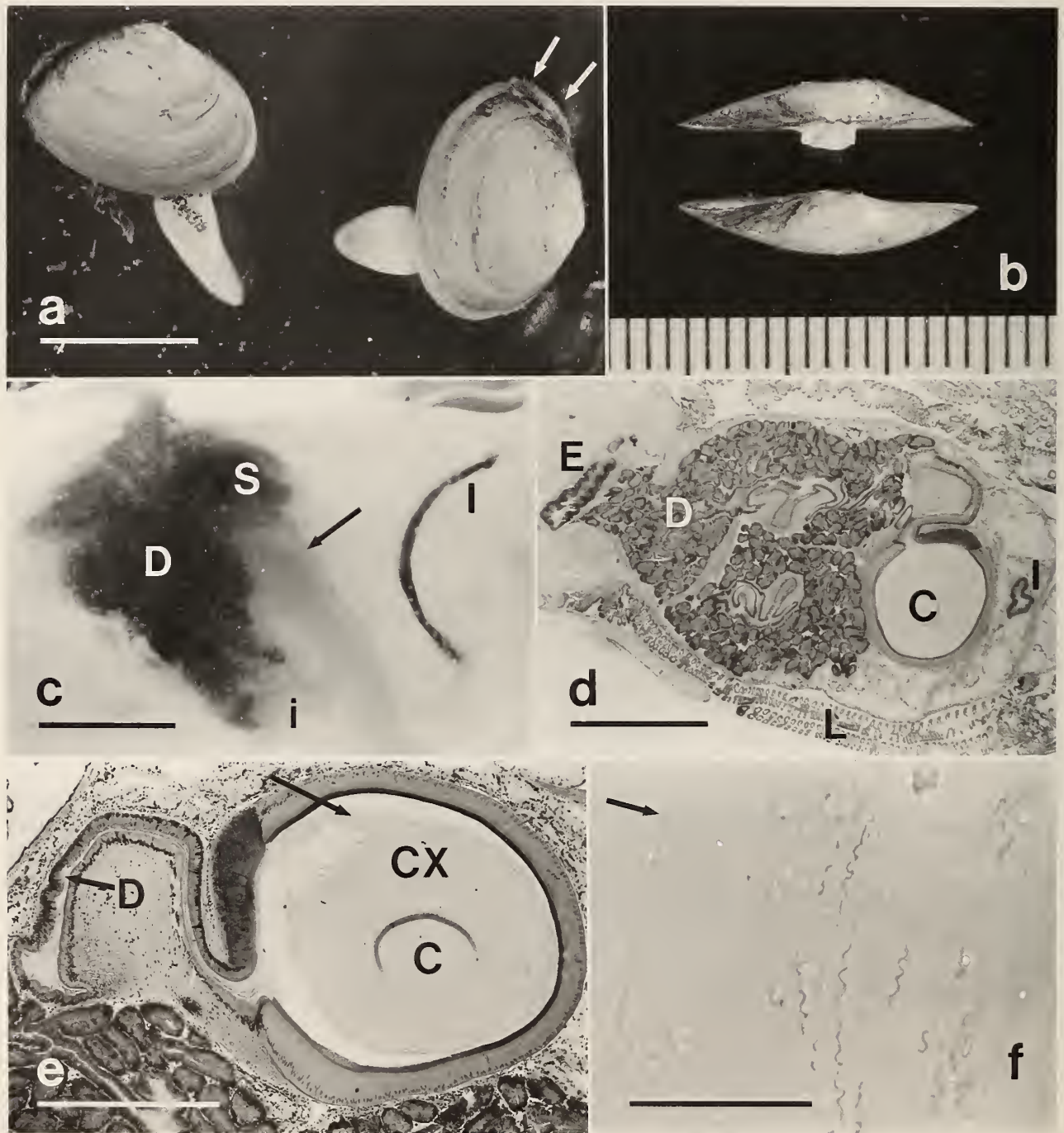


Figure 3

External and internal features of *Cryptomya californica*. a. Two specimens of *C. californica*, each with its muscular, ciliated foot extended. The short siphons (arrows) are indicated at the posterior end of one clam. Bar = 1 cm. b. Dorsal view of the valves of *C. californica*, with the chondrophore extending from the hinge of the left valve. The ruler is marked in 1 mm intervals. c. Dissection of the digestive organs of *C. californica*, as seen from the left side. The crystalline style, which is encased in a sac (arrow), protrudes into the stomach (S). Food is digested and absorbed primarily in the digestive diverticula (D). The intestine (i) loops twice as it descends from the right side of the stomach to an area near the ventral end of the style sac, where it curves dorsally (I) and carries waste materials to the anus. These organs are surrounded by gonad. Bar = 2 mm. d. Photomicrograph of a section of the

dorsal end against a prominent gastric shield in the stomach.

The style of a vivisectioned clam submerged in seawater was observed to rotate 7 to 30 rpm within its sac at water temperatures from 10 to 21°C respectively. The speed increased during several hours of observation, possibly owing to a rise in water temperature or a loss of ciliary control. The style rotated in a clockwise direction, the opposite direction noted by YONGE (1951), as seen from the dorsal end. I made these observations directly through the wall of the intact style sac, as a grain of black sand was fixed to the side of the style, and could be easily seen with each rotation. Even after the style was removed, style sac ciliary action continued for more than 5 h.

The crystalline style consists of a gelatinous, laminated cortex and a liquid core. Mucoïd material, apparently being applied to or wound around the outer surface of the style (as seen in the section in Figure 3e), appears to originate from the intestine and, possibly, secretory cells along the right side of the sac.

A crystalline style was always present in freshly collected clams, those exposed to air for 24 h, those kept submerged for long periods, and in clams that had been starved for 6 weeks.

Spirochete bacteria of the genus *Cristispira* (Figure 4f) were invariably found actively moving within the cortex and core of the entire style (Figure 3f). They were also observed in the stomach fluid, but not in the intestine or rectum. Freshly collected clams contained thousands of *Cristispira*. Although these bacteria appeared healthy and active, and were observed to divide, their populations within fed clams decreased steadily at rates of 5 to 12% per day after clams were removed from their natural habitat.

Sterilized styles demonstrated amylase activity by hydrolyzing starch. Bacilli isolated from the surfaces of unsterilized styles also hydrolyzed starch.

Nutrition

The microscopic examination of intestinal contents (Figure 4a) and fecal pellets (Figure 4b) from freshly collected clams showed that the animals normally ingest detritus consisting mostly of diatoms and bacteria, but sometimes containing dinoflagellates, crustacean and annelid setae,

sand, and even pollen grains. The digestive diverticula of fresh clams were usually green, presumably from chlorophyll of ingested algae (MATHERS, 1972). Carmine particles fed to clams passed quickly through the stomach into the intestine. No particles were observed in the digestive diverticula or the style. Clams that had been fed *Dunaliella salina* had algae (some still living) in the stomach 1 h after feeding. Chlorophyll had been incorporated into the core of the style in some cases.

Amebocytes

Rapidly moving amebocytes (Figure 4e) were often observed on the outside of the anterior end of the crystalline style. Such cells are elongate, measuring about 20 μm in length and 6 μm in width. The round nucleus, 2.3 μm in diameter, is centrally located. A large karyosome is in the middle of the nucleus. The cytoplasm contains numerous granules and vacuoles. These cells may be protozoan.

Gametes

The abundant gonads of *Cryptomya californica*, which fill most of the visceral cavity, contain either sperm (Figure 4c) or eggs (Figure 4d). The acrosomes of sperm are 5 μm long, tapered, and slightly curved. Including the flagellum, sperm measure 45 μm in length. The mature eggs are somewhat oblong, measuring 65 μm long and 53 μm at the widest point. There is a round, eccentric nucleus which is 30 μm in diameter and contains a large, round, eccentric nucleolus measuring 13 μm across. The abundant cytoplasm contains numerous inclusions (DOHMEN, 1983; LONGO, 1983; RAVEN, 1958).

DISCUSSION

Cryptomya californica occupies a nearly identical niche in the Oregon estuaries studied as it does in Monterey Bay, California. Dense populations of these clams are present in large areas of marine bays and lower estuarine sandy mudflats, especially in communities dominated by the ghost shrimp *Callinassa*. Because of its short siphons, deeply buried *Cryptomya californica* cannot have direct access to the surface of the sand. The animals are, therefore, usually embedded in the walls of tunnels of other burrowing or-

digestive organs lying immediately below the stomach (dorsal view). The crystalline style (C) is in a sac anterior to the ascending intestine (I) and posterior to the digestive diverticula (D) and the esophagus (E). At this level, the descending intestine is connected along its left portion to the style sac. They separate at about 1 mm below the stomach. The extensive lamellae (L) are also shown. H and E stain. Brightfield. Bar = 1 mm. e. Photomicrograph of a cross section of the crystalline style and style sac. The style has a liquid core (C) and a laminated cortex (CX). As seen from this dorsal view, the style rotates clockwise, propelled by the cilia of the columnar epithelial cells of the sac. Style cortex material (arrow) seems to originate from the typhlosoles of the style sac. In this section, the descending intestine (D) is connected to the style sac. H and E stain. Brightfield. Bar = 0.5 mm. f. Detail of the style cortex from Figure 3e, showing the orientation of its contained spirochete bacteria, *Cristispira*. The arrow indicates the outer edge of the style. Phase contrast. Bar = 0.1 mm.

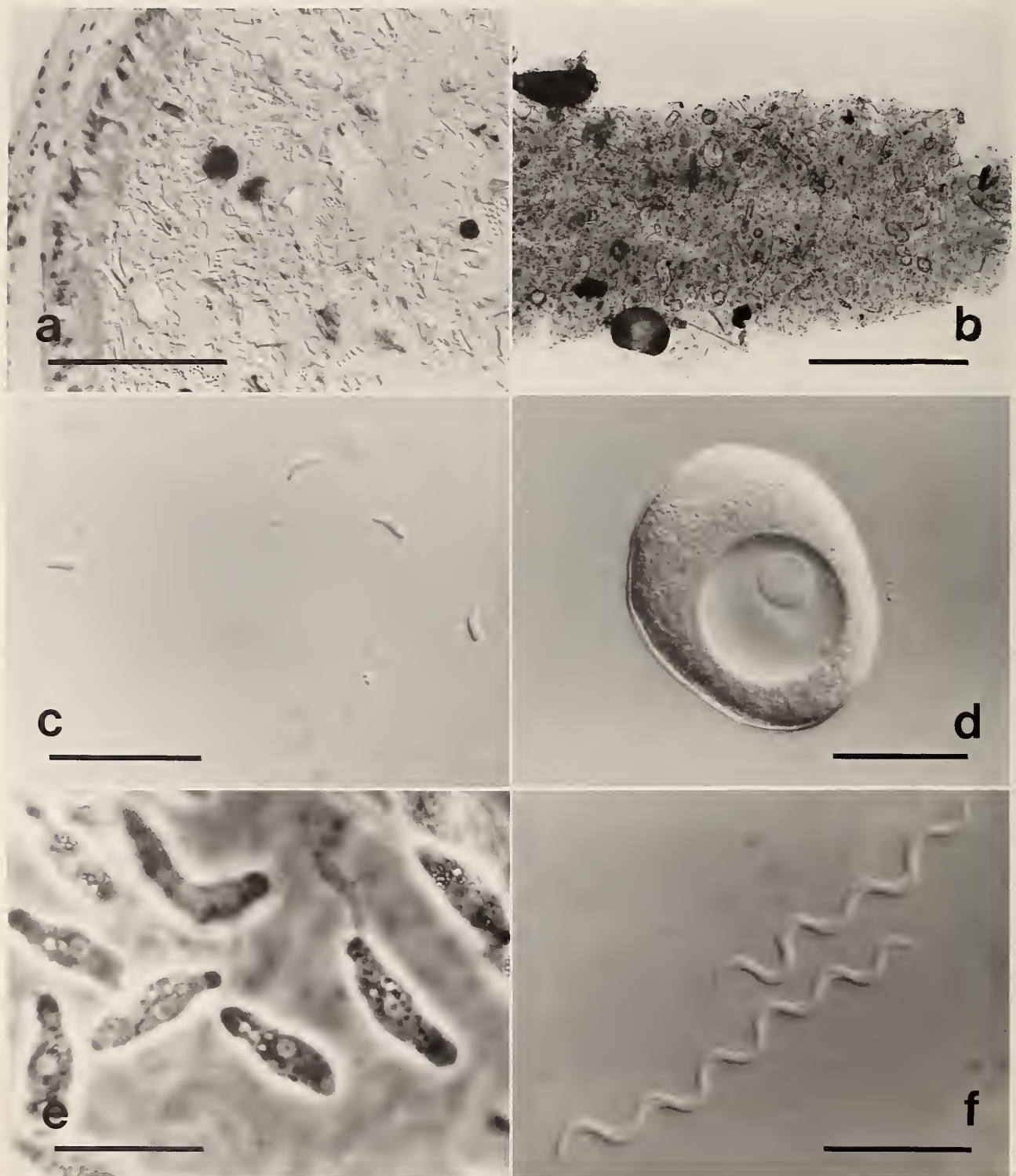


Figure 4

Cryptomya californica. a. A section through the descending intestine of a clam fixed immediately after collection, showing ingested detritus, especially diatom fragments. H and E stain. Nomarski optics. Bar = 70 μ m. b. A portion of a fecal pellet from a freshly collected clam. It contains the valves of diatoms and dinoflagellates, crustacean and

ganisms such as the shrimps *Callinassa californiensis* and *Upogebia pugettensis*, and (in California) the echiuran worm *Urechis caupo*. The siphons protrude slightly into the tunnel, and the water therein is the source of oxygen and food, and the depository for waste products.

The clams avoid predation and desiccation by living at safe depths (down to 50 cm) within the sand, where they undoubtedly take up residence early in their larval lives. The collapsing of tunnels by tidal forces, the incessant burrowing activities of *Callinassa* (MACGINITIE, 1934), or the searching of humans for edible clams and ghost shrimp for bait, may force *Cryptomya californica* to make frequent moves. The large cilia-covered foot, which can be extended through the pedal gape in the anteroventral portion of the mantle, the small slim shell, and the unencumbering siphons surely would facilitate movement through the sandy substrate.

The stomach clearly plays an essential role in the partial digestion and sorting of ingested substances (YONGE, 1923). As a result of ciliary activity, rotation of the crystalline style against the gastric shield, the release of enzymes from the style and digestive diverticula, and possibly some bacterial digestive action, several digestive processes are initiated in the stomach. First, large particles, such as diatoms, are shunted into the intestine, where degradation of contained organic material may be facilitated by the action of bacteria. Large numbers of motile bacilli were observed in fresh fecal pellets, and I noted that they actively congregated around masses of organic matter and diatoms contained in the pellets. Second, lysis of some plant cells takes place in the stomach. Third, much of the lysate and probably considerable amounts of bacteria are directed into the digestive diverticula to undergo further digestion and absorption. Lastly, some of the partially digested food is carried, along with quantities of mucus, into the style sac to form the liquid core of the style. The substance forming the laminated cortex of the style appears to be secreted by cells of the intestine and the typhlosoles along the right side of the style sac. While the core is continuously being replenished in the stomach, the anterior portion of the cortex is probably being dissolved there (MATHERS, 1974). The significance of the opening in the ventral end of the style sac is not clear. Some nutrient material may conceivably pass directly from the style sac into the body cavity through this aperture.

The crystalline style of *Cryptomya californica* is always present regardless of prolonged periods of submergence or exposure, or the presence or absence of food. *Callinassa*

beds are normally exposed only during tides below +0.3 m, and during most low tides the shrimps' tunnels probably contain enough water to permit *Cryptomya californica* to continue its respiratory and feeding activities (MACGINITIE, 1934). The persistence of the style is likely an adaptation to a nearly continuous feeding behavior.

MACGINITIE (1934) felt that competition for food between *Cryptomya californica* and *Upogebia* or *Urechis*, both of which are efficient plankton filterers, may explain why the clam seems to be more plentiful in burrows of *Callinassa*. The respiratory, burrowing, grooming, and sand-filtering activities of *Callinassa* not only circulate food-laden seawater through the burrow during high tides, but also stir up detritus (mostly diatoms and bacteria) during low tides. The alimentary canals of clams that I collected were always full of detritus.

Cryptomya californica normally has thousands of *Cristispira* in the stomach and matrix of the crystalline style. It seems that this population of spirochetes must be continuously replenished by ingestion of bacteria from the environment, as their numbers steadily decrease in clams removed from their natural habitat, even though the size of the styles does not decrease. The majority of the *Cristispira* are probably first incorporated into the core of the style as mucus is drawn from the stomach into the style sac. Afterwards, they make their way into the cortex, the substance of which they are able to partially liquify. They can be observed moving actively back and forth in liquid-filled channels apparently of their own making. I have observed these bacteria dividing *in situ*, but their growth rate within the style probably cannot keep up with attrition. Most are probably lost through the intestine, although none were identified there in this study. The invariable presence of a large, active population of spirochetes in the styles of freshly collected clams suggests that the bacteria may aid in the digestion of food materials ingested by the host. Upon degradation, however, they may also serve as a source of nutrition for the clam.

The crystalline style possesses the starch-hydrolyzing enzyme amylase. The release of this enzyme in the stomach assists in the digestion of plant materials normally consumed by *Cryptomya californica*. Gram negative bacilli, possibly *Vibrio* spp., which are always present in the stomach and style sac, also produce starch-hydrolyzing enzymes. Thus, at least part of the enzyme found in the style may be of bacterial origin. In my opinion, there is some validity to each of the following hypotheses: (a) that the crystalline style is an organ that stores digestive enzymes

annelid setae, plant material (including pollen grains), sand, and bacteria. Brightfield. Bar = 250 μm . c. Sperm of *C. californica*. Nomarski optics. Bar = 20 μm . d. An egg from *C. californica*, with its large round nucleus, prominent nucleolus, and extensive cytoplasm. Nomarski optics. Bar = 30 μm . e. Living, active amebocytes *in situ* on the outer surface of the crystalline style. Numerous cytoplasmic inclusions are visible. Phase contrast. Bar = 20 μm . f. Living *Cristispira* sp. *in situ* within the matrix of the crystalline style. Nomarski optics. Bar = 20 μm .

needed during feeding, (b) that it is itself a site where some digestion takes place, and (c) that some nutrients may be stored within its matrix for subsequent use during periods of food scarcity.

Amebocytes are often present on the outer surface of the anterior half of a style taken from a fresh clam. These cells are very active and contain numerous cytoplasmic inclusions. If they are indeed of clam origin, which remains to be shown, then presumably they act as scavengers maintaining the style and style sac. They may transport nutrients to other portions of the body.

The majority of the body cavity is filled with gonad, and immense numbers of sperm or eggs are produced. Although I observed fecund specimens in May, no seasonal data are available. Gametes are probably shed directly into the tunnels of *Callianassa* and other mud-dwelling organisms. The feeding activities of crustaceans, worms, mollusks, and gobies within the tunnels no doubt contribute greatly to the attrition of embryos and larvae (MACGINITIE, 1934) of *Cryptomya californica*.

ACKNOWLEDGMENTS

I thank John Baross, James Carlton, Carol Cogswell, Daniel Gleason, Suzanne Hamilton, Harrison Howard, Tena Lawry, Bayard McConnaughey, James McLean, Norman McLean, Richard Morita, Sonja Rasmussen, Paul and Lynn Rudy, and Donald Wimber for their kind assistance during this research.

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